

ANOMALOUS OCCURRENCES OF THE LOWER PALAEOZOIC BRACHIOPOD *SCHIZOCRANIA*

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ABSTRACT. There are rare occurrences of Ordovician and Silurian species of the inarticulate brachiopod *Schizocrania* attached to orthoconic cephalopod shells. These were probably transported considerable distances prior to their deposition in onshore sediments, in which *Schizocrania* is not normally found. Relationships between host and encruster are discussed with a view to elucidating both encrustation sequences and inferred ecological associations.

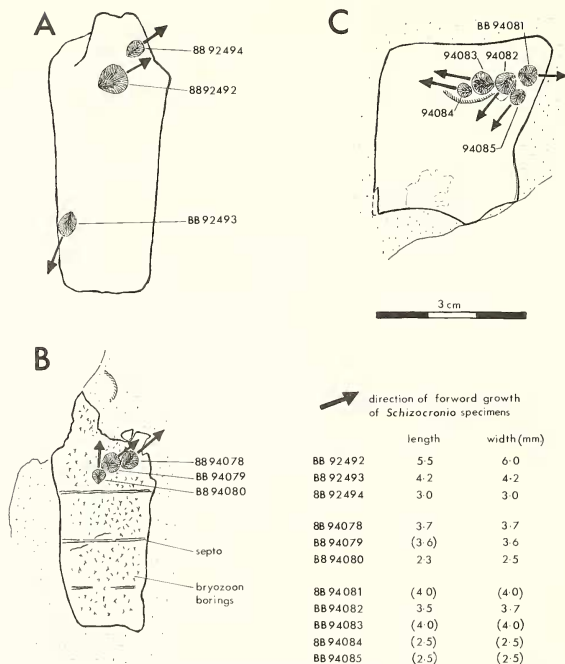
DURING the course of studies of Upper Llanvirn, Ordovician (MGL) and Whitcliffian, Silurian (DDJA) successions in the Anglo-Welsh region, we noted rare occurrences of orthocones with *Schizocrania* (Trematidae) attached to either the inner or outer walls of their body chambers; in both cases the associated elastic sediments are of a coarse arenaceous type associated with demonstrably shallow-water facies (Williams 1953; Antia 1979). Havlíček (1972, p. 230) reported that the Upper Ordovician trematid *Ptychopeltis nicola* Perner from Bohemia '... lived attached only to the cylindrical shells of orthocone nautiloids'; he also noted that its ancestor *P. hornyi* Havlíček sometimes encrusted orthocones. We therefore consider that these examples of apparent host-specific relationships may be paralleled elsewhere amongst the Trematidae (e.g. *Schizocrania*) by similar associations between host and encruster.

MATERIAL

The Upper Llanvirn specimen is an incomplete, poorly preserved internal mould of a body chamber of an orthoconic nautiloid of unknown taxonomic affinity. It was recovered from a shell-bed in the upper part of the Flags and Grits Formation of the Ffairfach Group exposed at Coed Duon, 3 km south of Llangadog, Dyfed (Grid Ref. SN 709256), where it lay parallel to bedding. The orthocone has three specimens of *Schizocrania* cf. *salopiensis* Williams attached to the inner surface of the body chamber; the brachial valves all face inwards (text-fig. 1A) but show no obvious preference for any particular attachment site although two of the specimens are aligned subparallel to each other near the anterior end.

The Whitcliffian specimens are represented by poorly preserved fragmentary moulds of *Orthoceras* sp. (diameters c. 20 mm and > 30 mm respectively) from the Lower Whitcliffe Beds of Mortimer Forest, south of Ludlow (Grid Ref. SO 497725) and the Upper Whitcliffe Beds near Broadstone Farm (SO 544900). The older specimen, an internal mould of a large portion of the conch (text-figs. 1B, 2B) has three specimens of *S. striata* (Sowerby) attached to the anterior part of its external surface. The specimens all occur close to each other on the exposed section of the orthocone mould which faces downwards from the undersurface of a bedded unit; relative to the final entombment position of the orthocone the *Schizocrania* specimens occur on its 'underside' and following the dissolution of the cephalopod shell have become impressed on to the preserved mould. The younger (upper Whitcliffian) specimen consists of the internal and external moulds of a curved fragment of a large body chamber; it has five poorly preserved specimens of *S. striata* attached to its inner (concave) surface which faces downwards. The specimens are aligned transversely, parallel to the peristome (text-figs. 1, 2C).

The lectotype (Geol. Surv. Mus. No. 6631) of *S. striata* (Sowerby) from the Leintwardinian-Whitcliffian beds of Delbury, Salop (Grid Ref. SO 501854) is the only other known British *Schizocrania* which we have discovered attached to an orthoconic nautiloid fragment; the specimen is attached to the convex surface of the free part of a septum, probably the last one; it differs from the other examples in its larger size (length 9 mm) and posterior attachment site (text-fig. 2A).



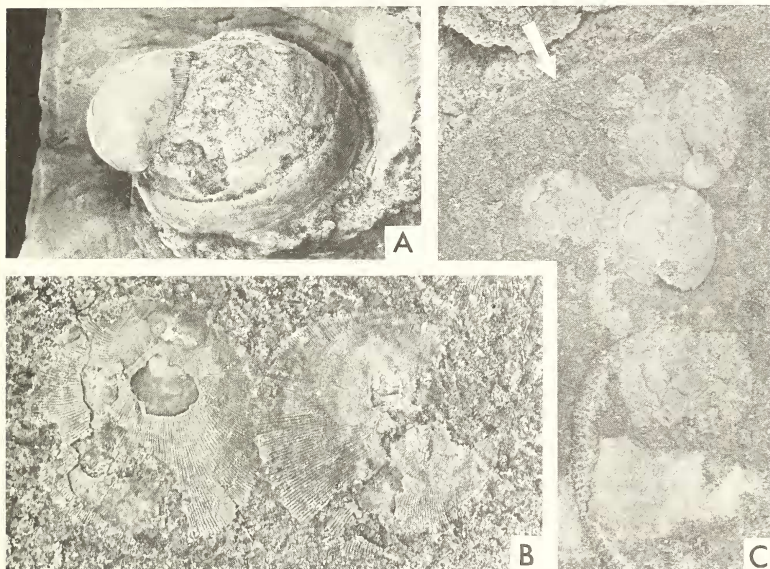
TEXT-FIG. 1. Scale drawings of *Schizocrania* encrusted orthoconic nautiloids from Upper Llanvirn strata exposed near Llangadog, Mid Wales (A) and from lower (B) and upper (C) Whitcliffe strata exposed near Ludlow, Salop. All *Schizocrania* specimens have British Museum numbers, specimens BB94078-94080 are attached to the outer surface of the shell mould (B) whilst the remaining specimens are attached to the inner surfaces of the shell moulds. Approximate length, width measurements, listed bottom right.

OBSERVATIONS AND INTERPRETATION

All twelve of these *Schizocrania* specimens exhibit only their convex brachial valves facing away from the cephalopod shell surface. *Schizocrania* is known to attach to substrates by its flat pedicle valve (Hall and Whitfield 1875; Rowell in Williams *et al.* 1965, p. H283). However, pedicle valves are exceptionally rare, being either altogether absent from assemblages or hidden from view beneath the brachial valve. The three orthocone specimens shown in text-fig. 1 indicate that the anterior edge of the phragmacone was the preferred encrustation site for all but two of the *Schizocrania* specimens. The orientation of these *Schizocrania* inside the phragmacone and on the shell exterior is apparently not random since all adjacent shells are aligned with their umbones pointing in approximately the same direction (i.e. transverse or oblique to the orthocones' long axis).

The orthocones may have been encrusted while they were alive and mobile, or when they were dead and floating, or dead and semi-buoyant, being washed around on the sea floor, or dead and settled on the sea floor, or, finally, when being reworked.

In addition to the numerous examples of fossil cephalopod (ammonoid) encrustation recorded from Mesozoic assemblages (e.g. Seilacher 1960; Meischner 1968) and the few broadly analogous Lower Palaeozoic examples involving orthoconic nautiloids (Holland 1971; Havlíček 1972), we have noted Ordovician and Silurian collections containing several varied and undescribed examples of orthocone encrustation (e.g. National Museum of Wales specimen NMW 79. 5G. Map loc. 771; Hunterian Museum specimens S.25129/1-3 and S.25114 a/b). *Schizocrania* is ornamented by numerous radial capillae (Williams 1974, p. 44). According to Williams and Wright 1963, p. 19 and Williams and Rowell (*in Williams et al.* 1965, p. H81) such radial ornament probably supported setal follicles at the commissure, and it is reasonable to assume that *Schizocrania* was particularly setiferous. Sudarson (1969, p. 65) noted that *Discinisca* larvae have well-developed principle setae and that 'there may be a prolonged larval stage . . . with chaetae increasing in number to facilitate floatation'. Both the *Schizocrania* species discussed here exhibit high capillae densities at the same



TEXT-FIG. 2. *Schizocrania striata* lectotype showing attachment to mould of orthocone septum from upper Ludlow beds, Delbury, Shrops., $\times 3$. B, Detail of *S. striata* specimens BB94078 (left) and BB94079 (right) from Lower Whitcliffe Beds, Mortimer Forest, Ludlow, $\times 12.5$; see also text-fig. 1B. C, *S. striata* specimens BB94081 (top) to BB94085 showing attachment to orthocone body chamber fragment, the edge of which is arrowed, from Upper Whitcliffe Beds, Broadstone farm, Ludlow, $\times 6$. Text-fig. 1C is a scale-drawing of the counterpart of this specimen.

growth stage (i.e. 10–12 per mm, 5 mm antero-medially of the dorsal umbones) and probably therefore had a juvenile epiplanktic stage.

Holland (1971, p. 18) considered that strophomenid (aegeromenid) and rhynchonellid (*Microsphaeridorhynchus nucula*) brachiopods might have attached to living orthocone hosts but concluded that due to the size of the brachiopods this was 'unlikely'. Havlíček (1967, p. 21) demonstrated the attachment of epiplanktic strophomenids to the 'stems of algae' (Havlíček 1967, p. 21). He subsequently suggested (Havlíček 1972, p. 230) that aegeromenids attached to live orthocones and considered that inarticulates such as *Ptychopeltis incola* 'were attached to the shells of living nautiloids' (Havlíček 1972, p. 230) whilst related trematids attached both to orthocones and other specific 'freely moving organisms' (Havlíček 1972, p. 229). An orthocone encrusted with *Conchiolites* (Ordovician) was described by Prantl (1948, p. 6). Seilacher (1954, 1968) concluded (1968, p. 284) that the preferentially orientated epizoans on this specimen were adjusted to the 'head-on motion of their host'. Both Havlíček (1972, p. 230) and Seilacher (1968) suggested that preferred orientation of encrusters is of prime importance in testifying to pre-mortem attachment. This suggests that the majority of known *Schizocrania* specimens were attached at various stages in the orthocone's post-mortem history. Although Havlíček (1972, p. 229) presumed that aegeromenid brachiopods such as those depicted by Holland (1971, fig. 1*b*) attached to live orthocones, direct evidence for this is insubstantial. Although these authors, and Bergström (1968) have shown such brachiopods attached in rows along orthocones and 'algal stems' such arrangements do not constitute the type of preferred orientation referred to above.

Since modern spirorbids are known to be host specific and capable of seeking a preferred attachment site and orientation (Knight-Jones 1951), it is almost certain that the occurrence of fossil spirorbids aligned along the growth margins of orthocones (Holland 1971) indicates a comparable relationship. This may mean that the similar alignment of *Schizocrania* specimens noted here (text-fig. 1) could also be indicative of a host-specific relationship. Such a contention tends to be supported by our observation that the Anglo-Welsh *Schizocrania* have not been found attached to any other host organisms and would also offer a possible explanation for the virtual absence of pedicle valves, which could have either remained attached to a host when the brachial valve disarticulated, or become obscured during fossilization by the substrate to which they were attached.

The *Schizocrania* on the internal surface of the body chambers of the Llanvirn and upper Whitcliffian specimens indicate encrustation beginning no earlier than the post-mortem drifting phase (following decay of mantle lining the body chamber) but prior to the infilling of the body chamber. Interpretation of the lower Whitcliffian orthocones' pre-entombment history is problematical; it could have been encrusted at any one of a number of stages in its history as a live or dead mobile organism. However, since the *Schizocrania* are attached to its 'underside' they must have settled and had time to grow prior to its final entombment in this position. The *S. striata* lectotype must have become attached to the posterior side of its septal substrate after the separation of the orthocone's body chamber from the remaining posterior part of the shell (i.e. at a relatively late stage in the orthocones' post-mortem history).

On the lower Whitcliffian orthocone the internal mould (text-fig. 1*b*) is covered by numerous irregular markings consisting mainly of small elongated raised protruberances averaging about 0.1 mm in height and width and between 0.3 and 0.7 mm in length. These apparently represent the internal moulds of bryozoan borings on the inner surface of the orthocone shell although it is not altogether clear whether some of the flatter or even slightly indented markings may not result from the fossilization of external borings. In any event where the *Schizocrania* shells are slightly broken, and around their edges, it is evident that the borings affect the orthocone shell beneath. Unfortunately the absence of a counterpart of this specimen renders this evidence inconclusive.

Distribution of Schizocrania

The Llanvirn orthocone and *Schizocrania* discussed here are virtually the only representatives of these taxa known from the predominantly arenaceous and rudaceous Ffairfach Group of the Llandeilo area. Since *S. salopiensis* is common in pencontemporaneous, argillaceous successions

elsewhere in South Wales and the Welsh Borderlands (Williams 1974; Bassett *et al.* 1974, p. 9; Lockley and Williams, in press) where there are different benthic and pelagic faunas (i.e. trilobites, graptolites, and cephalopods), it is reasonable to assume that the exotic Ffairfach occurrence may have been related to the drifting or migration of a stray cephalopod beyond the normal limits of its indigenous environment. Such post-mortem drifting of modern cephalopods is well known (House 1973; Kennedy and Cobban 1976; Hewitt and Pedlay 1978) and may result in individual specimens being transported for hundreds or even thousands of kilometres.

Similarly *S. striata* is rare in the Whitcliffe Beds of the Ludlow region where it constitutes only about 0.01 to 0.005% of the total fauna with specimens generally occurring in a fragmentary condition and random orientations. It is more common in unbioturbated, parallel-laminated, alternating light and dark siltstones (rhythmites) of deeper-water facies (e.g. Upper and Lower Leintwardinian Beds, Holland *et al.* 1963, p. 154; Lawson 1973, p. 274) and is recorded only rarely in shallow-water bioturbated siltstones (Facies B *sensu* Antia 1979). Again, the Whitcliffian cephalopods drifted into inshore deposits from an offshore source, although limited evidence also points to later phases of encrustation (e.g. lectotype). Williams (1969, p. 143) discussed the potential range of larval dispersal and its bearing on brachiopod migration during the Ordovician. Clearly his suggested figure (up to 250 km) is only a fraction of the range potential for brachiopods capable of encrusting live or drifting orthocones.

Trematid hosts

Encrusting Trematidae such as *Schizocrania*, *Drabodiscina*, and *Ptychopeltis* appear to have been host specific. *S. salopiensis*, *S. striata*, and *P. incola* have hitherto only been observed attached to orthoconic nautiloids generally presumed to have been alive or floating at the time of their encrustation. Other members of the family, e.g. *P. hornyi* Havlíček and *D. grandis* Barrande, are commonly attached to conularids which are considered by Havlíček (1972) to have been mobile during life, and the American species *S. filosa* Hall frequently attached to the brachiopod *Rafinesquina* (e.g. Cooper 1956 and Rowell in Williams *et al.* 1965). With respect to trematid-nautiloid associations, it is intriguing to note that Titus and Cameron (1976) record *S. filosa* only in their deep-water *Geisonoceras* (Orthocerida) community. Dr. R. A. Hewitt and Mrs. D. Evans (pers. comm. 1979) inform us that they know of no Silurian or Ordovician examples of cephalopod encrustation by brachiopods other than those reported here, which is suggestive of host-specific relationships.

CONCLUSIONS

Faunal associations with abundant *Schizocrania* in the Ordovician and Silurian of the Anglo-Welsh region are almost invariably confined to argillaceous deep-water facies where species of the genus are represented almost exclusively by assemblages of brachial valves. Such exceptionally disproportionate valve ratios are considered to result from their encrusting habits which might account for the obscuring or removal of pedicle valves. Known associations between trematid encrusters and hosts such as those reported here and elsewhere (e.g. Havlíček 1972; Rowell in Williams *et al.* 1965) point to some form of host-specific relationship between representatives of the family and other larger invertebrate hosts. Whether such relationships could be termed symbiotic, commensal, or parasitic is unclear because we lack evidence which demonstrates that hosts were encrusted during life. However, we can establish that encrustation of orthocones, which may in some cases have begun during their life, often began no earlier than the post-mortem drifting phase, and may have continued or begun at a time when the orthocones were resting or rolling on the sea floor. Since encrustation of many of these orthocones could not have taken place when they were in the final 'resting' position it must have occurred during the middle phases of their pre-entombment history.

The following suggestions on the time of encrustation can be made: (1) The encrusting *Schizocrania* noted here are not currently known to attach to non-orthocone skeletal components within the deposits from which they were recovered and are therefore likely to have settled

preferentially on orthocone shells prior to their final deposition. (2) The apparent high-density, orderly clustering of *Schizocrania* towards the anterior of the conch suggests that possibly the orthocone was colonized as a specific host whilst it was floating. (3) Since both *Schizocrania* and its nautiloid hosts are normally indigenous to sparsely fossiliferous, low-density offshore facies, it is probable that encrustation occurred in an offshore region before the orthocones finally became entombed in more diverse, fossiliferous, onshore facies where *Schizocrania* is invariably rare. This inference is supported by the observation that the setiferous *Schizocrania* may well have been adapted to a prolonged larval stage which would have enhanced its chances of encountering a suitable encrustation site. If *Schizocrania* even occasionally encrusted orthocones in a manner analogous to the attachment of epiplanktic aegeromenids to buoyant organisms noted by Bergstrom (1968), then the combined effect of nautiloid mobility during life and drifting after death would offer an explanation for exceptionally widespread occurrences of certain kinds of brachiopods.

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